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The potential of increased nitrogen supply to mitigate growth and yield reductions of upland rice cultivar UPL Ri-5 caused by *Meloidogyne graminicola* (1)

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Summary – Effects of *Meloidogyne graminicola* and nitrogen applications on growth and yield of upland rice cultivar UPL Ri-5 were studied in two glasshouse experiments. Plant height, shoot weight, leaf area, root weight, depth of rooting, and number of panicles and grains were reduced by the nematode. Grain yield was reduced by 30-70 % when the number of infective juveniles present around young seedlings at transplanting *(Pi)* was ⩾ 375. Total nitrogen in shoots decreased by 10-31 % at maximum tillering and by 14-20 % at flowering when 375 ⩾ *Pi* ⩾ 7500. Nitrogen concentration in shoots was not reduced. Root nitrogen concentration increased by 70-140 % at flowering and by 101-145 % at maturity with 375 ⩾ *Pi* ⩾ 7500. The nitrogen concentration in roots was positively correlated with *Pi* and the number of juveniles recovered from the roots. Nitrogen application increased growth and yield whether plants were infested by the nematode or not. However, because the percentage of yield loss remained approximately constant for a given *Pi* across the range of nitrogen quantities applied, nitrogen applications did not reduce the relative nematode effect.

Résumé – ***Capacité des apports d'azote à réduire les diminutions de croissance et de rendement causées par* Meloidogyne graminicola *au cv. UPL Ri-5 de riz pluvial*** – Les effets de *Meloidogyne graminicola* et d'applications d'azote sur la croissance et le rendement du riz pluvial cv. UPL Ri 5 ont été étudiés au cours de deux expériences en serre. La hauteur des plants, le poids des parties aériennes et des racines, la surface foliaire, la profondeur d'enracinement et le nombre de panicules et de grains sont diminués par le nématode. Le rendement est réduit de 30-70 % lorsque le nombre de juvéniles de second stade présents à la transplantation autour des jeunes plantules *(Pi)* est supérieur ou égal à 375. L'azote total des tiges et des feuilles est réduit de 10 à 31 % au stade de tallage maximum et de 14 à 20 % à la floraison lorsque *Pi* est compris entre 375 et 7500. Le taux d'azote dans les tiges et les feuilles n'est pas diminué alors que dans les racines il augmente de 70 à 140 % à la floraison et de 101 à 145 % à la récolte, pour les mêmes *Pi*. Le taux d'azote dans les racines est positivement corrélé avec *Pi* et avec le nombre de juvéniles extraits à partir des racines. Des applications d'azote augmentent la croissance et le rendement des plants infestés. Cependant, le fait que le pourcentage de perte de rendement reste à peu près constant pour une *Pi* donnée, quelle que soit la quantité d'azote appliquée, indique que l'apport d'azote ne supprime pas l'effet du nématode.

Key-words : *Meloidogyne graminicola,* nematode, nitrogen, pathogenicity, rice, yield loss.

The rice root-knot nematode, *Meloidogyne graminicola* is mainly distributed in South and Southeast Asian countries (Bridge *et al.,* 1990). It is suspected to suppress yield on rainfed upland, rainfed lowland, and deepwater rice (Bridge & Page, 1982; Bridge *et al.,* 1990; Jairajpuri & Baqri, 1991). In India, *M. graminicola* is considered as the second economically important nematode pest of rice next to *Hirschmanniella* spp. (Jairajpuri & Baqri, 1991). Rao and Biswas (1973) estimated that grain yield was reduced by 2.6 % for every 1000 nematodes present around 12-day-old seedlings. A reduction of 70 % in grain yield has been reported for irrigated rice cv. IR 36 grown under upland conditions when 1000 *M. graminicola* were present around young seedlings (Plowright & Bridge 1990). Rao *et al.* (1988) observed that the nitrogen concentration in roots and shoots was decreased in rice plant infested with *M. graminicola*. On the other hand, accumulation of nitrogen in the roots has been observed in pepper (Shaffiee & Jenkins, 1963) and tomato (Hunter, 1958; Maung & Jenkins, 1959) infected with *Meloidogyne incognita*. Bergeson (1966) made the hypothesis that root-knot nema-

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tode may have a direct parasitic effect by withdrawing and accumulating nitrogen at the expense of the top part and thus limiting its development.

We conducted two glasshouse experiments using upland rice cultivar UPL Ri-5 : *i)* to study the effect of *M. graminicola* on growth and yield and on the distribution of nitrogen in roots and shoots; and *ii)* to evaluate the potential of increased nitrogen supply to mitigate the reduction in growth and yield caused by the nematode.

Materials and methods

Meloidogyne graminicola used in both experiments were originally collected from Central Luzon, Philippines, on irrigated rice. They were cultured on UPL Ri-5 under upland conditions. Second-stage juveniles (J2) were obtained by placing infected roots in a mistifier. Only J 2 collected during 24 h periods were used.

The soil used in both experiments was an upland topsoil containing 40 % clay, 37 % silt, and 23 % sand. Its pH was 6.7 and has 19.5 ppm available P (Olsen) and 1.025 meq K/100 g. It was sterilized with methyl bromide 15 days prior to its utilization.

Seeds of UPL Ri-5 were pregerminated for 5 days in trays. Five-day-old seedlings with uniform growth were selected and a single seedling was planted in each pot.

Experiment 1

The first experiment was conducted in PVC pots (10 cm diam. and 65 cm long) filled with 7.5 kg of soil moistened with water to approximately field capacity. Ammonium sulfate at a rate of 80 kg N/ha (0.75 g/pot) was applied in three equal splits at transplanting and 28 and 52 days after transplanting (DAT). Six inoculum levels *(Pi)* of *M. graminicola* – 0, 75, 375, 750, 3750, and 7500 nematodes per plant – were used; they were considered as treatments. Second-stage juveniles were introduced in the first 15 cm of the soil, around the seedlings, in eight splits at transplanting and 2, 4, 6, 8, 10, 12, and 14 DAT. The initial weight of each pot was recorded. To determine evapotranspiration, the pots were weighed and watered every other day to enable them to reach their initial weight. To compensate for the amount of water fixed within the plant tissues and to maintain the soil at approximately field capacity, the quantity of water contained in each pot was adjusted at maximum tillering, booting, and flowering by adding the quantity of water in the plant tissues calculated between the beginning of the experiment and these different stages. To avoid interaction between treatments, the different treatments were considered as blocks. To avoid block position effect, the position of the blocks was randomized every other day. To avoid the factor position of the plant within the block, the position of each plant within a block was randomized every other day. Within a block, plants were arranged with a 20×10 cm spacing to simulate farmers' field spacing. Each block was surrounded by one row of border pots to simulate a closed canopy.

Plant development was assessed by measuring plant height and counting the number of tillers every other day. From each treatment, seven plants were harvested at four development stages : maximum tillering at 48 DAT, booting at 78 DAT, flowering at 84 DAT, and maturity at 110 DAT. For each sampling time, the following parameters were recorded : plant height; numbers of tillers and panicles; fresh weight of stems, leaves and roots; dry weight of stems, leaves and roots; root length; vegetative leaf area; flag leaf area; and nitrogen content of stems, vegetative leaf, flag leaf, and roots. Analyses of nitrogen contents were performed by the IRRI Analytical Service Laboratories using Kjeldahl digestion (Varley, 1966). At maturity, additional parameters were included : number, length and weight of panicles; number of filled and unfilled grains; weight of grains per plant; and 100 grain weight. For each sampling time, the nematode population densities of *M. graminicola* were estimated by placing half of the root system in a mistifier for 7 days. Data were analyzed using linear and second-order polynomial regressions between actual numbers of juveniles of *M. graminicola* inoculated per plant and their *ln (Pi + 1)* on one hand and the average values of all the parameters recorded on the plants on the other. Linear and second-order polynomial regressions between all the parameters recorded on the plants were also tested.

Experiment 2

The second experiment was conducted in PVC pots (20 cm diam. and 60 cm long) filled with 15 dm^3 of soil moistened with water to approximately field capacity. Thereafter pots were watered daily to field capacity. Six inoculum levels *(Pi)* of *M. graminicola* – 0, 150, 750, 1500, 7500, and 15 000 J 2 per plant – were used. They were introduced in the first 15 cm of the soil, around the seedlings, in five splits at transplanting and 3, 6, 9, and 12 DAT. Four levels of nitrogen were used – 0, 40, 80, and 160 kg N/ha (0, 0.5, 0.9, and 1.9 g per pot). Nitrogen was applied in the topsoil as ammonium sulfate in three equal splits 10 DAT, at maximum tillering, and at panicle initiation. All possible combinations between nematode inoculum levels and nitrogen levels were performed resulting in 24 different treatments.

Treatments were replicated six times and arranged in a randomized complete block design with 20 cm spacing between pots. For each plant, the date of flowering was recorded when half of the panicles had flowered. At maturity, the following parameters were recorded : number of tillers, number of panicles, dry top weight, fresh root weight, depth of rooting, number of filled and unfilled grains, and grain yield.

The number of nematodes in the roots was estimated by cutting the whole root system of each plant into 1 cm

7 days in a mistifier. Data were analyzed by analysis of variance (ANOVA) and multiple regressions were used to illustrate the relationships between the different parameters recorded, *Pi,* and the quantity of nitrogen applied.

Results

EXPERIMENT 1

Grain yield was strongly positively correlated ($p < 0.01$) with different growth parameters of the rice plant : flag leaf dry weight ($r = 0.91$); depth of rooting ($r = 0.89$); flag leaf area ($r = 0.82$); stem dry weight ($r = 0.82$); root fresh weight ($r = 0.81$); flag leaf nitrogen ($r = 0.80$); plant height ($r = 0.79$); and dry ($r = 0.79$) and fresh weight ($r = 0.78$) of the vegetative aboveground part of the plant. Except for fresh weight of roots at maximum tillering, all these growth parameters were significantly linearly negatively correlated ($p < 0.05$) at maximum tillering, flowering, and maturity stages with initial number of *M. graminicola.* Grain yield was also strongly ($p < 0.01$) negatively correlated with nitrogen concentrations in the roots ($r = 0.83$) that was positively correlated ($p < 0.05$) with *Pi.*

Polynomial regressions of the second order gave the best correlations observed between the *ln* of the initial number of nematodes inoculated [*ln (Pi + 1)*] and the different vegetative parameters at different growth stages. The vegetative above ground dry weight was strongly correlated ($p < 0.01$) with *ln (Pi + 1)* at maximum tillering and flowering (Fig. 1 A, B); the two variables were also correlated ($p < 0.05$, $R^2 = 0.86$) at maturity. A negative correlation was also observed between plant height and *ln (Pi + 1)* at flowering and maturity (Fig. 1 C, D) but not at maximum tillering, while the vegetative leaf area was correlated ($p < 0.05$) with *ln (Pi + 1)* at maximum tillering and flowering stages (Fig. 1 E, F) but not at maturity. Other aboveground growth parameters which correlated ($p < 0.05$) with initial number of nematodes include the flag leaf areas at flowering and maturity (Fig. 2) and the fresh and dry weight of vegetative aboveground parts at all growth stages. Most of these aboveground growth parameters were drastically affected by the presence of *M. graminicola.* Plant height and fresh and dry weight of aboveground parts were reduced at all growth stages and all inoculum levels except at maturity when $Pi = 75$. With the exception of the plants harvested at flowering and inoculated with 75 and 750 nematodes, the vegetative leaf area was reduced at all growth stages and inoculum levels. Reduction of total flag leaf area by 20-75 % were observed at flowering and maturity at all inoculum levels greater than 75 nematodes per plant. The only growth parameter which was not correlated ($p < 0.05$) with *Pi* at any growth stage was the number of tillers.

The fresh root weight at maturity ($p < 0.01$, $R^2 = 0.97$) and the depth of rooting at maximum tillering and flowering (Fig. 3 A, B) as well as at maturity ($p < 0.05$, $R^2 = 0.71$) were negatively correlated ($p < 0.05$) with *ln (Pi + 1).* Depth of rooting was reduced by more than 25 % at all growth stages when nematode inocula were greater than 75 juveniles per plant. A positive correlation ($p < 0.05$) was observed between nitrogen concentration in roots and *Pi* at flowering and maturity stages (Fig. 3 C, D). With initial inoculum levels of 75, 375, 750, 3750, and 7500 nematodes per plant at flowering stage, the percentages of nitrogen in the roots were increased by 47, 70, 95, 102, and 140 %, respectively (Fig. 3 C). At maturity, with the same inoculum levels, these percentages were increased by 56, 100, 124, 145, and 129 %. Significant ($p < 0.05$) linear correlations were also observed between the percentage of nitrogen in the roots and the number of second-stage juveniles recovered per g of roots at maximum tillering ($R^2 = 0.70$), flowering ($R^2 = 0.67$), and maturity ($R^2 = 0.97$).

In vegetative aboveground parts of the plant, the total nitrogen was negatively correlated ($p < 0.05$) with *Pi* at maximum tillering ($R^2 = 0.68$) and flowering ($R^2 = 0.92$). However, at all growth stages, the total nitrogen in vegetative aboveground parts of the plant was correlated ($p < 0.05$) with dry weight of these parts but not with nitrogen concentration in the stems and vegetative leaves. Moreover, the nitrogen concentration in the stems and vegetative leaves was not correlated with *Pi.*

At maturity, strong ($p < 0.01$) positive linear correlations were observed between grain yield and its components : weight of 100 grains ($R^2 = 0.94$), number of filled grains per plant ($R^2 = 0.99$), and percentage of filled spikelets ($R^2 = 0.97$). In addition, significant ($p < 0.05$) negative linear correlations were observed between *Pi* and grain yield, weight of 100 grains, number of filled grains per plant, and number of panicles (Fig. 4).

Yield parameters were reduced by the presence of the nematode. Average grain yield was reduced by 6, 41, 59, 55, and 77 % when plants were inoculated with 75, 375, 750, 3750, and 7500 nematodes, respectively. The number of filled spikelets per plant was reduced by 50 % or more when $Pi \geq 750$. The weight of 100 grains was reduced by 13, 13, and 20 % with 750, 3750, and 7500 nematodes per plant, respectively. Reductions by 29 and 35 % in panicle numbers were observed with the two higher inoculum levels.

The average daily evapotranspiration considered between transplanting and maturity was correlated ($p < 0.05$) with *ln (Pi + 1)* (Fig. 5 A). It was also correlated ($p < 0.05$) with yield (Fig. 5 B) and its components and with all the aboveground growth parameters such as plant height (Fig. 5 C), fresh and dry weight (Fig. 5 D) of aboveground parts, and vegetative

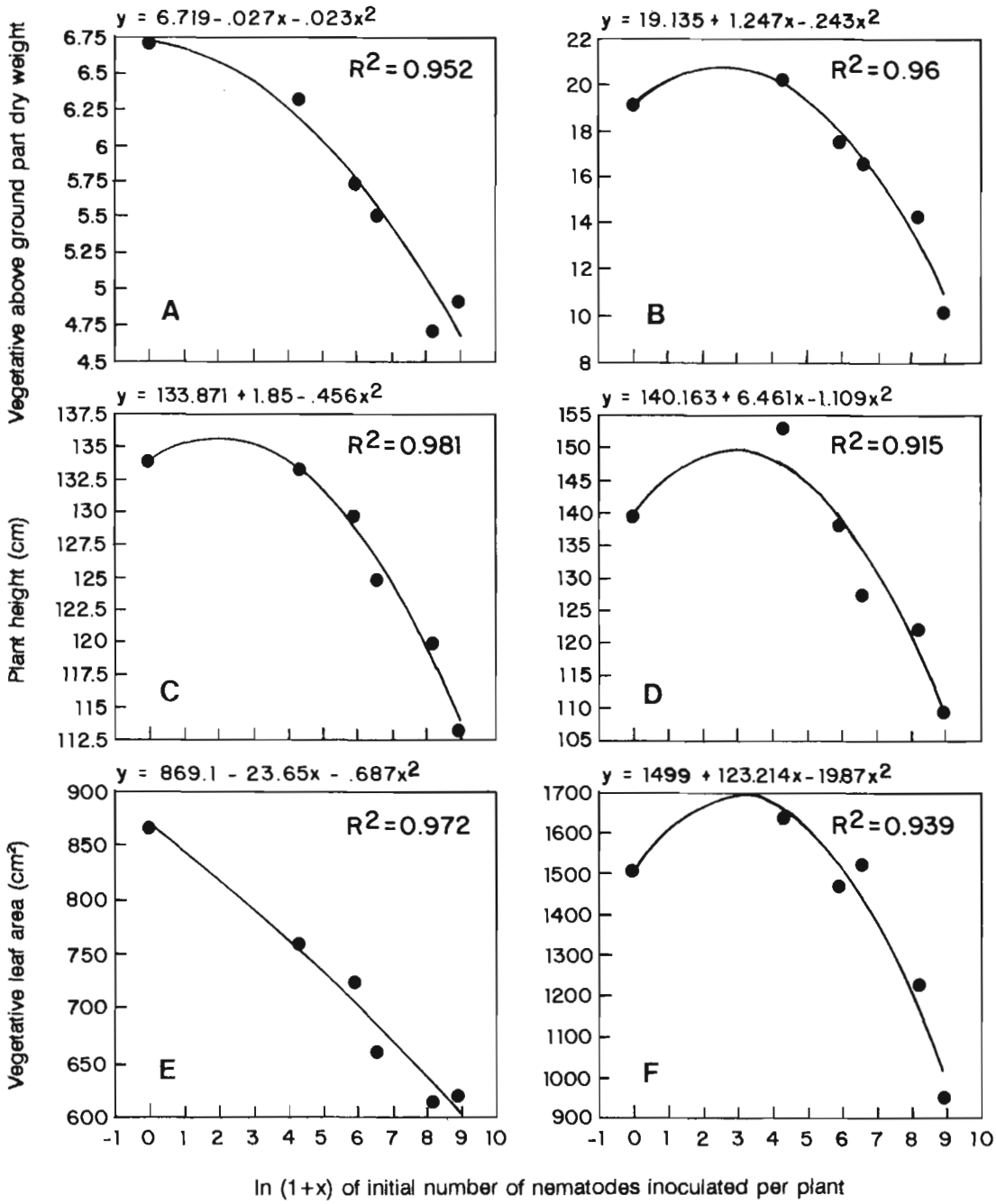

Fig. 1. *Effect of different inoculum levels of* Meloidogyne graminicola *on shoot dry weight (g/plant) at maximum tillering (A) and maturity (B), on plant height (cm) at flowering (C) and maturity (D), and on vegetative leaf area (cm²/plant) at maximum tillering (E) and flowering (D) stages of upland rice cv. UPL Ri-5.*

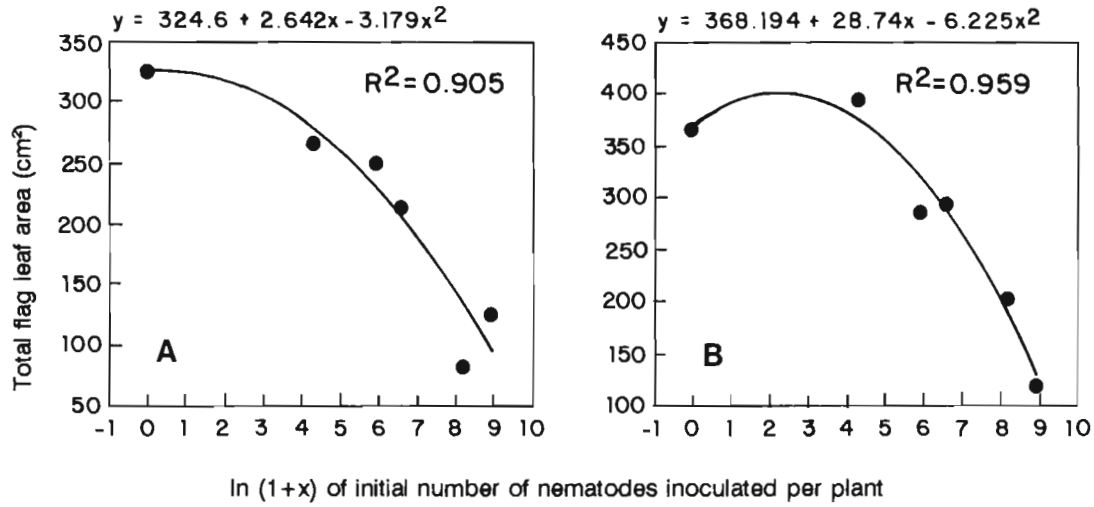

Fig. 2. *Effect of different inoculum levels of* Meloidogyne graminicola *on total flag leaf area (cm²/plant) of flowering (A) and maturity (B) stages of upland rice cv. UPL Ri-5.*

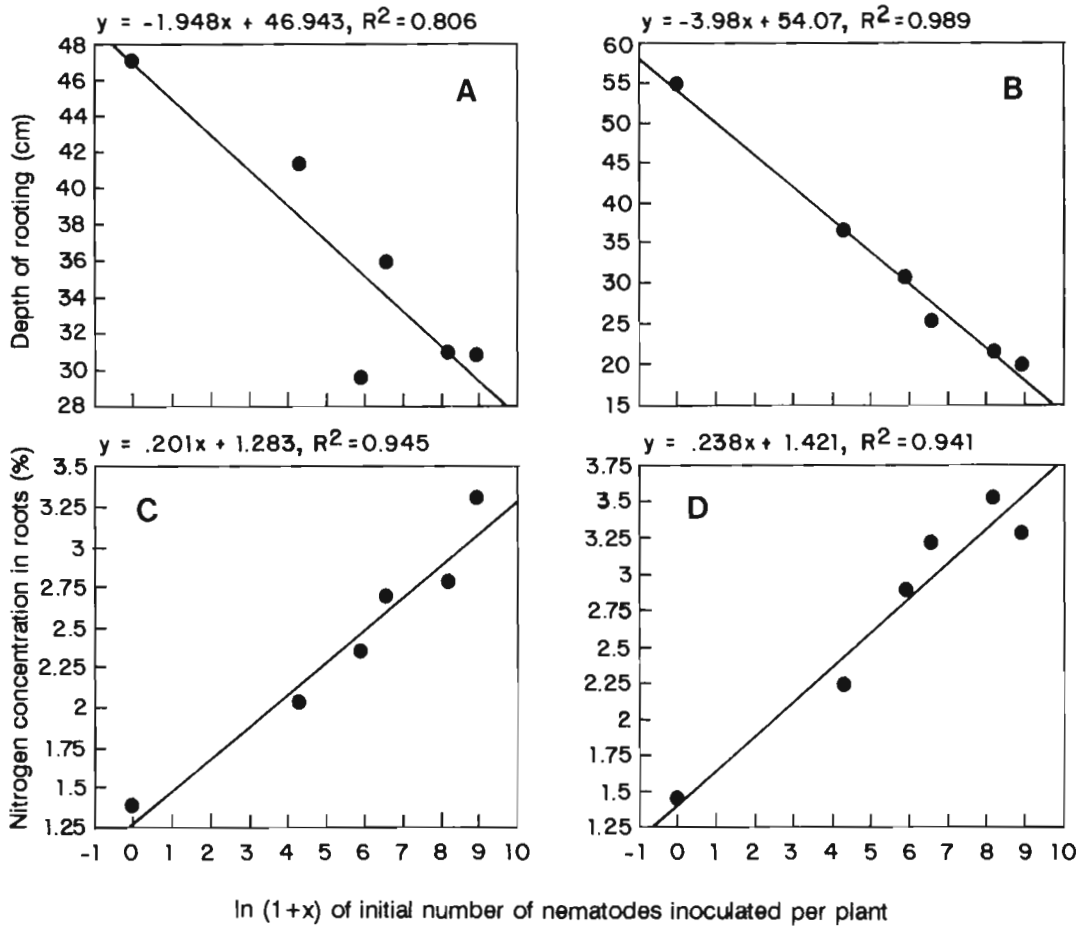

Fig. 3. *Effect of different inoculum levels of* Meloidogyne graminicola *on depth of rooting (cm) at maximum tillering (A) and flowering (B), and on nitrogen concentration (% dry weight) in the roots at flowering (C) and maturity (D) stages of upland rice cv. UPL Ri-5.*

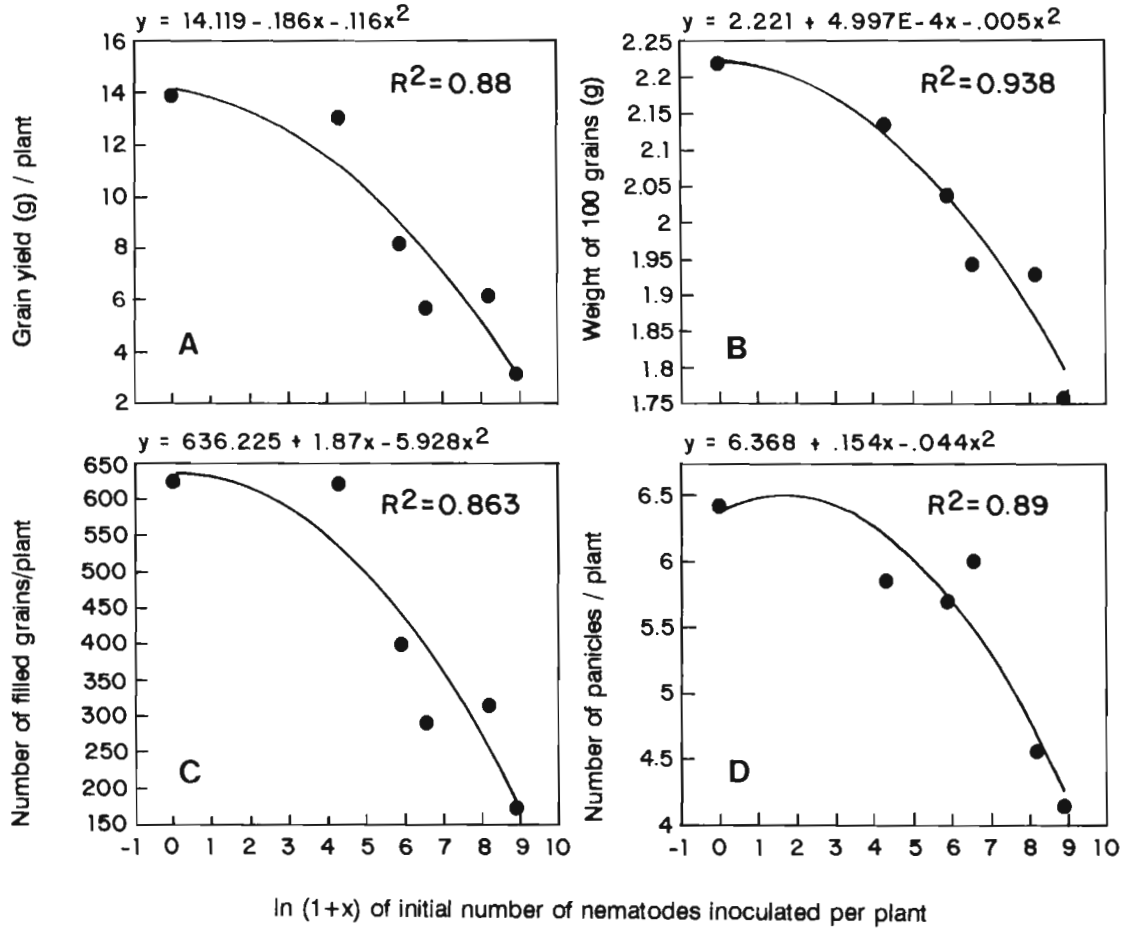

Fig. 4. *Effect of different inoculum levels of* Meloidogyne graminicola *on A : Grain yield (g/plant); B : Weight of 100 grains (g); C : Number of grains; D : Number of panicles at maturity of upland rice cv. UPL Ri-5.*

($R^2 = 0.721$) and flag ($R^2 = 0.859$) leaf areas. Similar results were obtained at flowering and maximum tillering.

The number of J2 recovered per root system was correlated with *Pi* at maximum tillering ($r = 0.90$, $p < 0.01$) but not at flowering ($r = 0.39$, $p > 0.05$) and maturity ($r = 0.18$, $p > 0.05$).

Experiment 2

Variations in plant height *(PH)*, number of tillers *(NT)*, dry weight of the shoot *(DWT)*, and number of days between sowing and flowering *(DF)* with different *Pi* and quantities (in kg/ha) of nitrogen applied *(N)* are illustrated in Fig. 6. ANOVA indicated highly significant effects of *Pi* ($p < 0.01$) and N ($p < 0.01$) on the variations of these parameters. There was no significant interaction effect *(Pi × N)* on variations of these parameters. *PH, NT,* and *DWT* were increased by nitrogen applications and decreased by the nematode. On the average, whatever was the initial nematode inoculum, *PH, NT,* and *DWT* were respectively increased by 9, 8, and 20 % when $N = 40$ kg/ha; by 6,13, and 41 % when $N = 80$ kg/ha; and by 10, 38, and 63 % when $N = 160$ kg/ha. Whatever was the amount of *N* applied, *PH, NT,* and *DWT* were respectively decreased by 2, 15, and 10 % when $Pi = 150$; by 7, 34, and 29 % when $Pi = 750$; by 4, 21, and 22 % when $Pi = 1500$; by 8, 17, and 28 % when $Pi = 7500$; and by 8, 30, and 37 % when $Pi = 15\,000$. Flowering occurred 4 days earlier when they received 80 or 160 kg N/ha but was delayed by 4 days when $Pi = 7500$ and 15 000.

The effects of *Pi* and N on PH (in cm), NT, DWT (in g), and DF are illustrated by the following multiple regression equations :

$PH = 141 - 1.5 \ln (Pi + 1) + 0.064\ N$ ($R^2 = 0.63$, $p < 0.0001$)
$NT = 15 - 0.49 \ln (Pi + 1) + 0.038\ N$ ($R^2 = 0.66$, $p < 0.0001$)

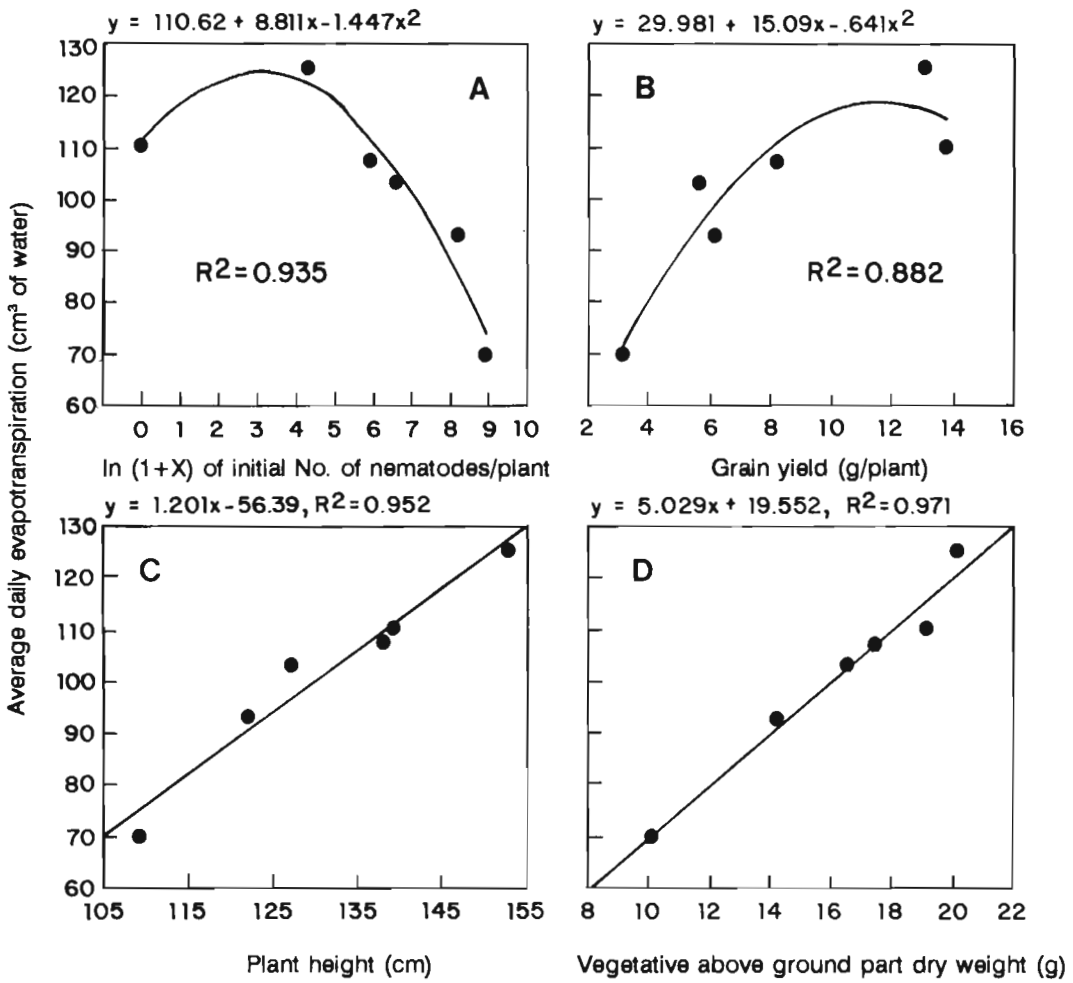

Fig. 5. *Relationships between number of* Meloidogyne graminicola *inoculated per plant (A), grain yield (g/plant) (B), plant height (cm) (C), and dry weight of shoot (g/plant) (D) at maturity and the average daily evapotranspiration (cm^3/day) of upland rice cv. UPL Ri-5.*

$DWT = 50.1 - 2.17\ ln\ (Pi + 1) + 0.138\ N\ (R^2 = 0.87,\ p < 0.0001)$

$DF = 85 - 0.38\ ln\ (Pi + 1) - 0.026\ N\ (R^2 = 0.55,\ p < 0.0002)$

On the average, fresh root weight *(FWR)* was increased by 12 % with $N = 80$ and 160 kg/ha; at the same time, depth of rooting *(DR)* was reduced by more than 11 % with the same quantities of nitrogen applied (Fig. 7). *FWR* and *DR* were reduced by more than 30 % when $Pi \geq 750$. ANOVA indicated a highly significant effect of *Pi* ($p < 0.01$) and a significant effect of *N* ($p < 0.05$) on the variations of these two parameters. There was no significant interaction effect *(Pi × N)* on these variations.

Effects of *Pi* and N on the variation of *FWR* (in g) and *DR* (in cm) are illustrated by the following multiple regression equations :

$FWR = 62.5 - 2.65\ ln\ (Pi + 1) + 0.064\ N\ (R^2 = 0.70,\ p < 0.0001)$

$DR = 63.7 - 2.84\ ln\ (Pi + 1) - 0.038\ N\ (R^2 = 0.75,\ p < 0.0001)$

Grain yield per plant *(GY)*, number of panicles per plant *(NP)*, number of grains per plant *(NG)*, and percentage of unfilled spikelets per plant *(% US)* obtained with different *Pi* and *N* are shown in Fig. 8. ANOVA indicated a highly significant effect of *Pi* ($p < 0.01$) and *N* ($p < 0.01$) on the variations of *GY*, *NG*, and *NP* but no significant effect on *% US*. There was no significant interaction effect *(Pi × N)* on these variations. *GY* and *NG* were increased by all nitrogen level applications. *GY* was increased by 36 % with $N = 40$ kg/ha, by 50 % with $N = 80$ kg/ha, and by 87 % with $N = 160$ kg/ha. *GY* was reduced by 30 % or more when $Pi \geq 750$. Maximum yield reductions – 75 % without *N*, 68 % with $N = 40$ kg/

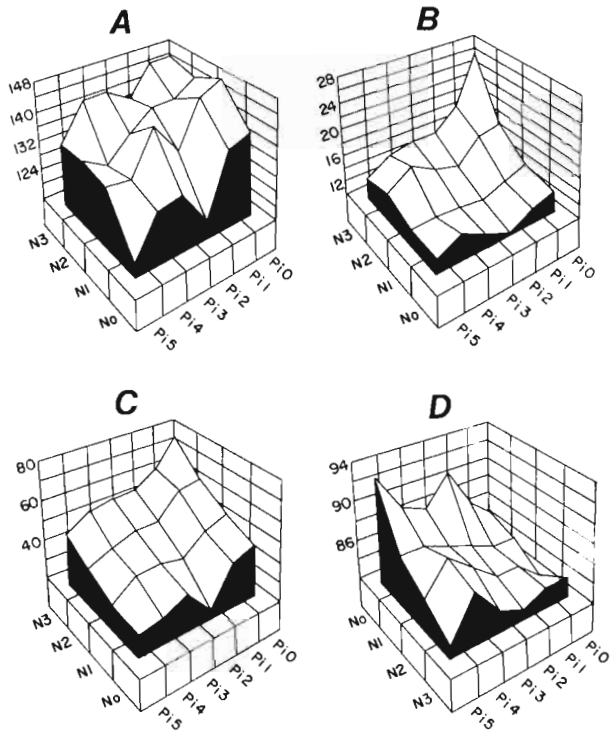

Fig. 6. *Variations of A : Plant height (cm); B : Number of tillers; C : Dry weight of shoot (g/plant); D : Date of flowering of upland rice cv. UPL Ri-5 grown with five different levels of* Meloidogyne graminicola *inoculated per plant at transplanting (Pi0 = 0, Pi1 = 150, Pi2 = 750, Pi3 = 1500, Pi4 = 7500, Pi5 = 15 000) and four levels of nitrogen inputs (N0 = 0 kg/ha, N1 = 40 kg/ha, N2 = 80 kg/ha, N3 = 160 kg/ha).*

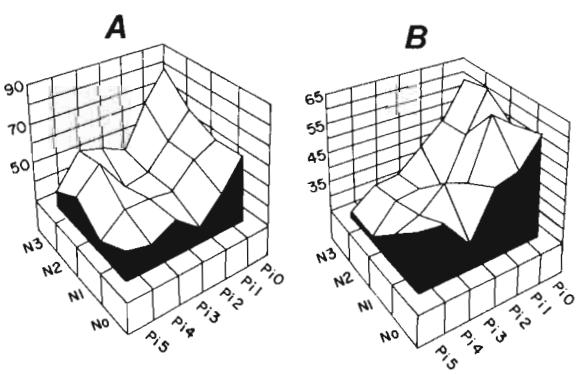

Fig. 7. *Variations of A : Fresh root weight (g/plant); B : Depth of rooting (cm) of upland rice cv. UPL Ri-5 grown with five different levels of* Meloidogyne graminicola *inoculated per plant at transplanting (Pi0 = 0, Pi1 = 150, Pi2 = 750, Pi3 = 1500, Pi4 = 7500, Pi5 = 15 000) and four levels of nitrogen inputs (N0 = 0 kg/ha, N1 = 40 kg/ha, N2 = 80 kg/ha, N3 = 160 kg/ha).*

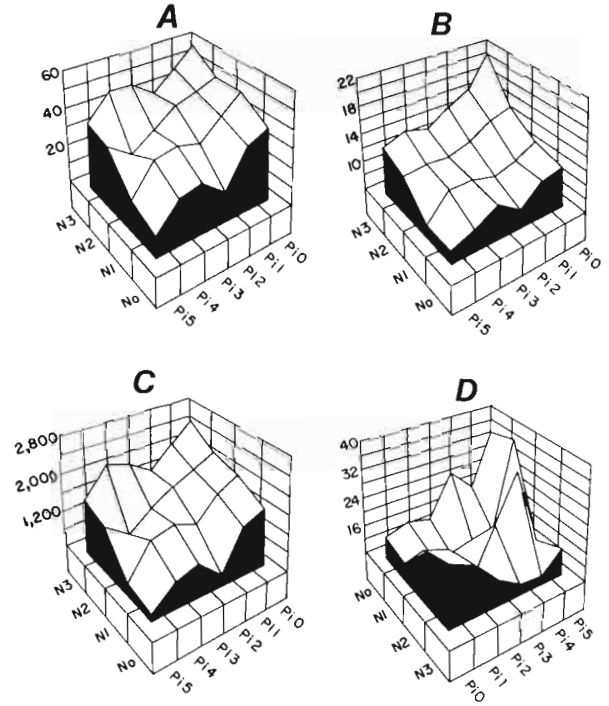

Fig. 8. *Variations of A : Grain yield (g/plant); B : Number of panicles; C : Number of grains; D : % of unfilled spikelets of upland rice cv. UPL Ri-5 grown with five different levels of* Meloidogyne graminicola *inoculated per plant at transplanting (Pi0 = 0, Pi1 = 150, Pi2 = 750, Pi3 = 1500, Pi4 = 7500, Pi5 = 15 000) and four levels of nitrogen inputs (N0 = 0 kg/ha, N1 = 40 kg/ha, N2 = 80 kg/ha, N3 = 160 kg/ha).*

ha, 35 % with N = 80 kg/ha, and 41 % with N = 160 kg/ha – were observed when Pi = 15 000. Almost identical variations were observed for NG. Average NP was increased by 10, 30, and 60 % with N = 40, 80, and 160 kg/ha, respectively. NP was decreased by 13 % with Pi = 150; by 20 % with Pi = 750, 1500, and 7500; and by 33 % with Pi = 15 000.

Effects of Pi and N on the variation of GY (in g), NP, and NG are illustrated by the following multiple regression equations :

$GY = 40.8 - 2.41 \ln (Pi + 1) + 0.126 N$ ($R^2 = 0.82$, $p < 0.0001$)
$NP = 12.9 - 0.52 \ln (Pi + 1) + 0.037 N$ ($R^2 = 0.86$, $p < 0.0001$)
$NG = 1718 - 98.9 \ln (Pi + 1) + 5.627 N$ ($R^2 = 0.82$, $p < 0.0001$)

ANOVA indicated that there was no significant effect of Pi and N on the variation of the weight of 100 grains and on the variations of number of second-stage juveniles observed per 3 g of root and per root system at maturity when Pi was greater than 0 (Table 1).

Discussion

All the aboveground characteristics in rice – plant height, dry weight of stems and leaves, vegetative leaf

Table 1. *Effects of different nitrogen and inoculum of* Meloidogyne graminicola (Pi) *levels on the number of second stage juvenile (J 2) recovered from the roots at maturity.*

	Nitrogen (kg/ha)							
Pi	0		40		80		160	
Number of J 2 per 3 g of root at maturity (thousand)								
0	0	*aA*	0	*aA*	0	*aA*	0	*aA*
150	20.1	*bA*	11.2	*bA*	9.8	*bA*	7.8	*bA*
750	12.3	*bA*	19.7	*bA*	3.3	*bA*	9.0	*bA*
1500	6.9	*bA*	7.6	*bA*	8.0	*bA*	12.9	*bA*
7500	10.4	*bA*	5.5	*bA*	4.9	*bA*	8.7	*bA*
15 000	6.1	*bA*	7.6	*bA*	8.0	*bA*	5.8	*bA*
Number of J 2 per plant at maturity (thousand)								
0	0	*aA*	0	*aA*	0	*aA*	0	*aA*
150	352	*bA*	188	*bA*	198	*bA*	119	*bA*
750	149	*bA*	267	*bA*	539	*bA*	136	*bA*
1500	95	*bA*	112	*bA*	106	*bA*	181	*bA*
7500	144	*bA*	79	*bA*	65	*bA*	172	*bA*
15 000	48	*bA*	82	*bA*	120	*bA*	57	*bA*

* Means of six replications. In a column, average number followed by a common lower case letter are not significantly different at the 5 % level by DMRT. In a row, average number followed by a common upper case letter are not significantly different at the 5 % level by DMRT.

area, flag leaf area – were reduced when plants were infested with *M. graminicola,* with the exception of the number of tillers in the first experiments. This reduction of the top growth of plants resulted in the typical stunting observed in rice infested by root-knot nematodes (Babatola, 1984; Plowright & Bridge, 1990). *M. graminicola* also reduced the root weight and the depth of rooting thereby limiting the ability of the plant to extract water and nutrients from the soil. The second-order polynomial regressions observed between *Pi* and top growth parameters suggest that low populations of *M. graminicola* may, to some extent, stimulate the growth of UPL Ri-5.

M. graminicola strongly reduced yield in both experiments. Maximum yield losses of 70 % were observed. Yield reductions equal to or greater than 30 % were always achieved when 375 or more second-stage juveniles were present around young seedlings at transplanting regardless of the quantity of nitrogen applied. *M. graminicola* may affect the formation and development of the reproductive organs of the rice plant during the reproductive and the ripening growth stages. The reduction in number of panicles and spikelets indicates that the nematode limits the initiation and development of panicle primordia. The increase in number of unfilled spikelets and the decrease in 100 grain weight in the first experiment indicate that *M. graminicola* may increase the sterility and limit the filling of the grains after heading.

Nitrogen applications resulted in growth and yield increases whether plants were infested by the nematode or not. However, the absence of interaction between *N* and *Pi,* observed in the second experiment, indicates that under the experimental conditions used, nitrogen application did not increase or compensate for nematode effects on plant yield and growth. Similar results indicating that damage caused by nematodes on rice is of the same amplitude regardless of fertilizer applications have been obtained in upland rice with *Meloidogyne incognita* (Diomandé, 1981) and irrigated rice with *Hirschmanniella oryzae* (Fortuner, 1977). In the second experiment, nitrogen application limited the depth of rooting. Because nitrogen was placed in the topsoil, the high nitrogen concentration in the upper part of the soil probably did not encourage the roots to grow deeper, preventing them escaping nematode infestation. This may be one of the causes of the inefficiency of nitrogen to compensate for the nematode effect.

In irrigated rice, yield depends mainly on the total quantity of nitrogen in shoots (Cassman *et al.,* 1993) that is related to shoot weight and concentration of nitrogen in shoots. In our first experiment, *M. graminicola* reduced the total shoot size and therefore the quantity of nitrogen in the shoots but not its concentration in the stems and leaves. Moreover, nitrogen concentration was increased in the roots and correlated with initial and final nematode populations. These results disagree with results obtained by Rao *et al.* (1988) who observed a decrease in nitrogen concentration in roots and shoots of rice infested with *M. graminicola.* However, accumulation of nitrogen in root-knot nematode-infected roots have been observed in pepper (Shaffiee & Jenkins, 1963) and tomato (Hunter, 1958; Maung & Jenkins, 1959; Bergeson, 1966). *M. graminicola* may have a direct parasitic effect by withdrawing and accumulating nitrogen at the expense of the top part and thus limiting its development.

Sedentary endoparasitic nematodes can upset plant-water relations (Evans *et al.,* 1977; Wilcox-Lee & Loria, 1986, 1987). In our first experiment, evapotranspiration was correlated with *Pi.* However, it was also correlated with all the top growth parameters. The observed reduction in evapotranspiration may have resulted from a reduction in growth caused by a withdrawal of nutrients or physiological changes induced by *M. graminicola.* This experiment does not allow us to conclude on the effect *M. graminicola* on water uptake and water flow between roots and top parts. It remains likely that effects on evapotranspiration were the result and not the cause of adverse effects of nematode infection.

At flowering and maturity, the number of second-stage juveniles recovered per g of root or per root system was not correlated with initial population. This indicates

that competition and overpopulation may limit nematode reproduction. Because the number of juveniles recovered at maximum tillering stage still correlated with *Pi*, it seems that in our first experiment this overpopulation occurred between maximum tillering and flowering. A similar observation was made by Plowright and Bridge (1990) with *M. graminicola* on rice.

Under the conditions that prevailed in our experiments, *M. graminicola* drastically reduced growth and yield of upland rice cultivar UPL Ri-5. Yield was reduced by more than 30 % when 375 or more infective juveniles were present around young seedlings. Yield reductions of up to 70 % were observed with $Pi \geqslant 7500$. Results suggest that a withdrawal and immobilization of nutrients by the nematode can be one of the causes of growth and yield reductions.

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